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A FIELD STUDY OF GROWTH AND REPRODUCTION IN *APLYSIA CALIFORNICA*[1]

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Some aspects of reproduction in the marine opistobranch *Aplysia californica* have been the subject of considerable research over the past ten years. Description of a cluster of neurosecretory cells in the central nervous system was followed by extensive work directed toward characterization of their secretory product, which was found to induce egg-laying (Arch, 1972; Arch, Earley, and Smock, 1976; Kupfermann, 1967, 1970; Pinsker and Dudek, 1977). Strummwasser, Jacklet, and Alvarez (1969) noted a yearly cycle both in egg-laying hormone production and in receptivity to the substance. Thus initial investigation of the reproductive cycle in *A. californica* was from the standpoint of its neurohormonal control.

To date, no long-term studies of natural populations of this species have been published. *Aplysia punctata,* found in the eastern Atlantic, has been more extensively investigated. A 16-month study of this species from Trearddur Bay, Anglesey (Carefoot, 1967a) led to the conclusions that *A. punctata* is an annual, breeding between May and October, with major settling in the autumn. The red alga *Plocamium coccineum* supplies a substantial part of the diet of the Trearddur Bay population (Carefoot, 1967a), in addition to supporting more rapid growth than several other algal species being consumed (Carefoot, 1967b, c).

A major difference between *A. punctata* and *A. californica* is size. While *A. punctata* rarely exceeds 80 g (Carefoot, 1967a), *A. californica* often exceeds 3000 g with a species record of 6800 g reported by MacGinitie and MacGinitie (1968). The growth rate and life span necessary to achieve such size have not been documented, nor have seasonal changes in abundance, weight, or reproductive

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activities of a natural population been reported. This paper describes the results of such an investigation.

Materials and Methods

This study was conducted between July 1972 and August 1975 at the University of California's Catalina Marine Science Center on Santa Catalina Island, 25 km off the California coast south of Los Angeles. Two field study areas were selected which were in close proximity to the marine laboratory and known to support subtidal populations of *A. californica* (subsequently referred to as *Aplysia*). Site 1 covered part of Bird Rock, a small island approximately 500 m from shore. The area investigated covered about 35 m of shoreline and extended to a depth of 8 m. The total area of ocean floor studied was roughly 5600 m^2. The sea bed sloped gently within the study area, but dropped more precipitously around the rest of the rock island.

Site 2 consisted of approximately 140 m of coastline starting inside Big Fisherman's Cove on Catalina Island, extending a short distance east along the coast and to a depth of about 8 m for a total sea bed area of approximately 2800 m^2.

Except for the collections described below, the *Aplysia* populations in these areas were protected from human disturbance.

Collections were made once each month at each site, beginning in July of 1972 at Site 1, and in June of 1973 at Site 2. A monthly collection at each site was continued through August of 1975. Each month, weather permitting, from two to five divers using SCUBA covered the bottom in a zigzag pattern between the depths of 1 and 8 m along the length of the study area (depths were approximate as indicated by divers' depth gauges). Because most specimens of *Aplysia* were found in water shallower than 5 m, on some dives the area below this depth was not searched. Each specimen of *Aplysia* encountered was collected. Divers rarely found animals weighing less than 20 g due to the searching techniques used, and the tendency of smaller animals to be camouflaged amidst algal fronds. The data on abundance and weight presented in this paper therefore exclude all newly metamorphosed specimens and most juveniles of less than 20 g.

From July of 1972 through March of 1973, the presence or absence of copulating individuals was noted during the monthly collections. From April 1973 through the end of the study period, additional data were collected on underwater slates during the dives. These included the number of animals paired or aggregated, and in many cases the number of animals in individual aggregations. Paired animals were usually copulating and were always in physical contact with one another. An aggregation was defined as a group of three or more specimens of *Aplysia* in physical contact with one another. Such groups generally included individuals engaged in egg-laying, copulation, or both. At any given time the aggregation could include (or on rare occasions be entirely composed of) animals not engaged in either of these activities (see also Kupfermann and Carew, 1974).

After collection, the animals were brought into the laboratory where each was weighed (after being placed on a paper towel for a few seconds to drain off excess water). Beginning in August 1973, each animal was tagged with a one-half inch Floy Tag (Floy Tag and Manufacturing, Seattle, WA), colored with waterproof marker and stamped with an identifying number or letter. A tagging gun was used to insert the tag through one of the parapodia. While in the laboratory, the animals were housed in aquaria supplied with a continuous flow of fresh sea water within 1° C of ambient ocean temperature. After being tagged and weighed, the animals were returned to the study site, usually within 24 hr of the time of capture.

Histological examination of gonads from *Aplysia* was performed each month from October 1973 through September of 1975. To assure a supply of gonads throughout the year and to conserve local populations, gonads were obtained from specimens of *Aplysia* sacrificed for neurophysiological research at the California Institute of Technology in Pasadena, California. These animals were obtained (through Pacific Biomarine Supply Co.) from Palos Verdes on the California coast about 25 km north of Catalina Island. These were maintained in a recirculating sea water system without feeding on a regular schedule of 12 hr of darkness alternating with 12 hr of light. The temperature was maintained at a constant 14° C.

The animals whose gonads were examined had been maintained under these conditions for an average of 11 days. Each animal was weighed after removal of excess water as described above. A piece of gonad (3 to 5 mm^2) was removed (preliminary measurements had shown that average oocyte diameter is uniform throughout the gonad) and fixed in Bouin's solution made with sea water. The tissue was then dehydrated, cleared, and embedded in Paraplast. Non-serial (usually every tenth section was retained) 5-mm sections were stained using Cason's modification of the Mallory-Heidenhain stain (Humason, 1967). The stained sections were examined microscopically, and oocyte diameter measured with an ocular micrometer. To establish a standard point of reference for measurement, only oocytes in which nucleoli were visible were measured. According to Thompson and Bebbington (1969), the nucleolus is prominent until the *Aplysia* oocyte has completely matured, at which time it disappears. Thus a slight bias against very large oocytes may be introduced by this method. The average diameter of the first 50 oocytes in which the nucleolus was visible was determined. Fixation seemed to have little effect on oocyte size, as the diameter of the largest oocytes measured (80 μm) was approximately the same as a newly laid egg. In extremely immature gonads, oocytes were small and difficult to measure with certainty. Based on initial measurements, an average value of 7 μm was assigned to the oocytes of such immature gonads. The number of animals sampled each month ranged from 5 to 20, but in 19 of the 24 months, ten or more animals were examined.

Results

Seasonal variation in weight

Figure 1 shows size-frequency distributions of all collections at Site 1 in which more than six animals were found. Presentation of the data in this form reveals some trends as well as the considerable variability in population structure from one year to the next. The tendency of small animals to appear in the winter and spring can be seen in 1973 and 1975. An increase in overall size during late spring and summer is evident in 1974 and 1975. Unpredictable fluctuations in size and numbers also occurred. In late winter and early spring of 1973, juveniles appeared as expected, and had begun to increase in size by May. In June, however, the population inexplicably disappeared and remained absent for the remainder of the summer and fall. A few animals appeared in December, and specimens of *Aplysia* in a range of sizes were present through the spring of 1974. The sizable component of small animals present in the spring of the preceding and succeeding years was absent.

Figure 2, which shows the trends apparent over the three-year sampling period, was generated by combining the data for each month throughout the sampling period. Each site is graphed separately, with each point representing the weighted average of the collections made during that month. Seasonal differences in the size of the animals are apparent. Highest weights were recorded during the summer months of June through August, while weights were generally lowest between February and May. There is also a significant difference in the weights of the populations found at the two study sites. These were compared by performing a

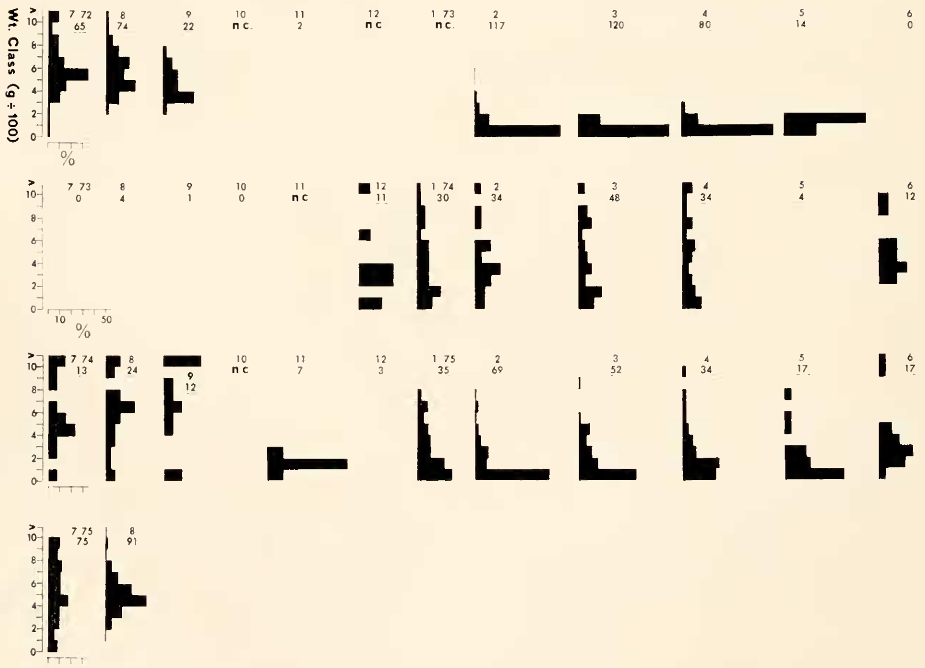

FIGURE 1. Size-frequency distribution of all collections at Site 1 in which more than six animals were found. The width of the figure corresponds to the percentage of animals found in each size class. The uppermost number is the date, while the underlined number immediately below it shows the number of specimens of *A. californica* collected that month. N.C.: no collection.

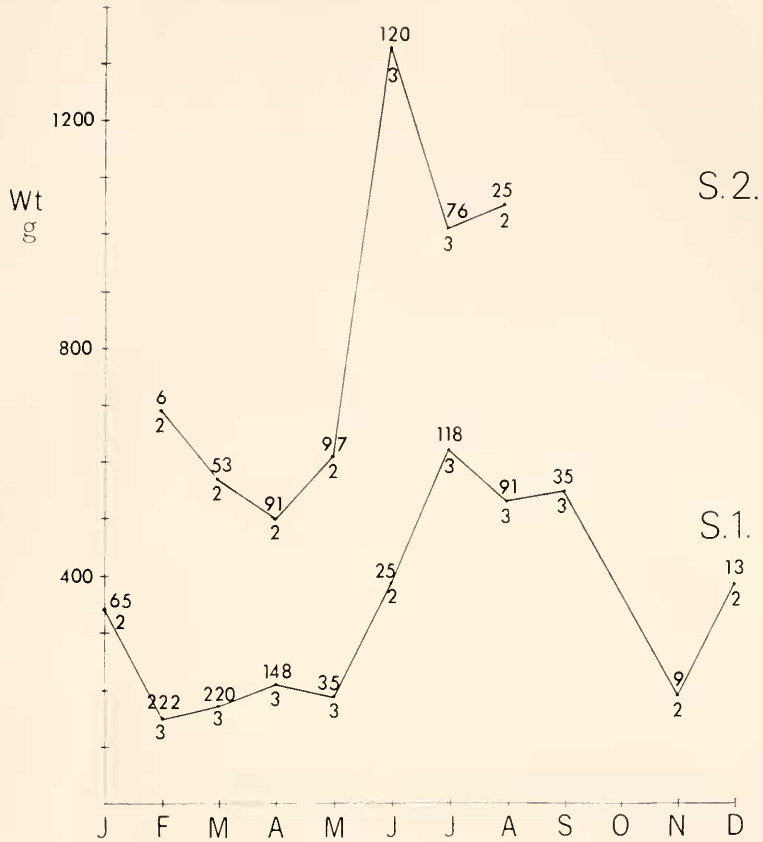

FIGURE 2. Average weights of specimens of *A. californica* collected at each study site, plotted by month. S. 1: Site 1; S. 2: Site 2. The upper of the two numbers associated with each data point is the total number of animals collected during that particular month throughout the study period. The lower number is the number of years in which samples were collected during that month. Only months in which six or more specimens of *A. californica* were collected are graphed.

paired *t*-test on the average weights for the ten individual months in which more than six animals were collected at each site (two-sided paired *t*-test; $t = 3.6$, $P < 0.01$). The two study sites differed in the availability of food algae readily consumed by *Aplysia*. Site 1 was dominated by beds of the surfgrass *Phyllospadix* to a depth of about 3 m. This plant is not normally consumed by *Aplysia* (Winkler and Dawson, 1963; personal observation). Below 3 m, the giant kelp *Macrocystis* predominated. Numerous other algal species were present on the rocky substrate including several which have been reported to serve as food for *Aplysia* (Leighton, 1966). Of these, only two were readily consumed under laboratory conditions, *Laurencia* and *Plocamium*. Neither of these algae was abundant at Site 1. Site 2 supported (among many other algal species) large beds of *Plocamium* between the depths of 1 and 4 m. Below this depth, *Macrocystis* predominated.

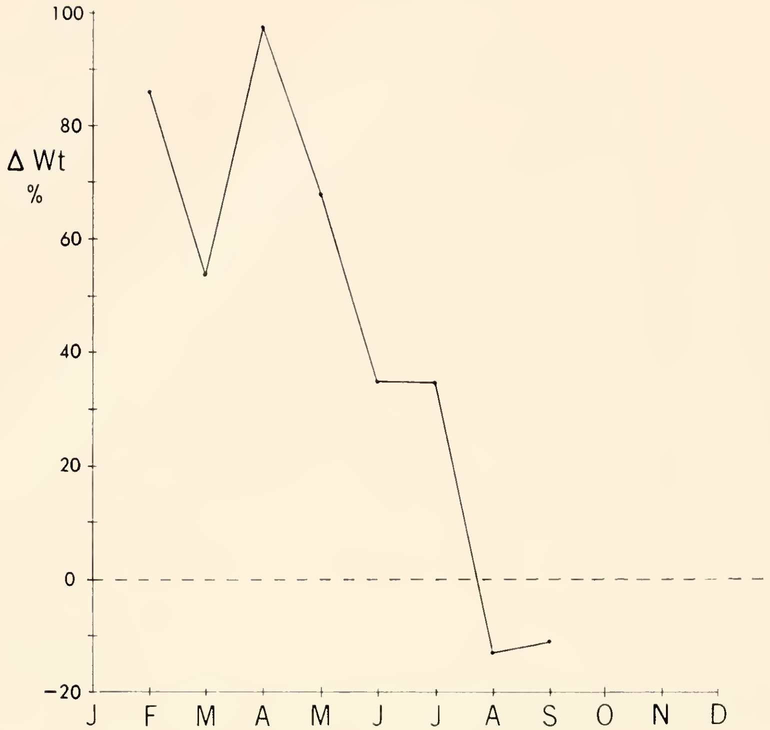

FIGURE 3. Graph of data from Table I. Changes in weight are expressed as percentages of initial body weight and plotted according to month. Data from both study sites collected throughout the tagging program are presented. Only months in which five or more animals were recaptured are graphed.

The average weights of animals used at Caltech also show seasonal variation, in spite of attempts by Pacific Biomarine Supply Co. to provide animals of roughly uniform size. Figure 6 shows that animals were smallest during late winter and early spring, while maximum weights were reached during the summer and fall. This parallels the trend seen in the populations studied on Catalina Island.

Tagging and recapture

A total of 154 specimens of *Aplysia* were recaptured between June of 1973, when the tagging program was initiated, and August of 1975, when the study was completed. Altogether, 728 animals were tagged during this period. Of those recaptured, 101 had been tagged the previous month. Only these were used to generate Figure 3, to best illustrate the growth trends typical of individual months. In Figure 3, field weight changes have been expressed as percentages of beginning body weight. Data have been combined for animals collected at both study sites, and for the same month throughout the tagging period. Only months in which five or more individuals were recaptured are graphed. Since few animals were found in winter (Fig. 4) there were few recaptures between October and January. Again, strong seasonal trends are evident, with the maximum percent increase occurring in late winter and early spring when the animals are relatively small, and decreasing as the average weight of the population increases. A net loss of weight occurred during August and September. Table I shows the number of recaptured animals which had gained or lost weight during each month of the year. Weight loss was almost never observed between January and June, but after June, the majority of animals recaptured had lost weight.

In some instances, the same individual was recaptured more than once, providing information on the weight changes which individuals experience with age and season. These cases reveal that this species is capable of considerable growth during a single month. One animal from Site 2 gained 910 g between February and March of 1975, and an additional 1178 g between March and April of that year. Two animals which were captured first in the spring and later in the summer each showed an initial weight gain, followed by summer weight loss.

In this study, specimens of *Aplysia* were tagged with considerable success. Nine animals were recaptured after four or five months, indicating that some individuals spend a considerable time within a limited area. This species is capable of traveling relatively long distances, however. Kupfermann and Carew (1974) found that *A. californica* could easily cover a distance of 75 m (net) in a two-day period. Because many animals could have moved out of the study areas from one month to the next, recapture data from this study were not dependable for population size estimates.

Seasonal changes in abundance

It was noted during collections that the abundance of *Aplysia* seemed to vary seasonally, with a maximum during the spring, and a nearly total disappearance during the months of October and November. Abundance was estimated by determining the number of animals captured per unit effort, with one unit of effort defined as one diver-hour. The trend that emerges when data taken throughout the study are graphed by month is shown in Figure 4A. While few or no animals were found during regular monthly dives between October and December, juveniles ranging from 1 mm to 2 cm in length were found on *Plocamium*

TABLE I

Weight changes under field conditions.

Month	N	Initial Wt. (mean, g)	Wt. Change (mean, %)	No. gaining	No. losing
Jan	2	380	42	2	0
Feb	5	475	85	4	1
Mar	16	386	54	16	0
Apr	11	695	98	11	0
May	7	545	68	7	0
Jun	12	865	30	10	2
Jul	15	1060	35	7	8
Aug	31	644	−13	3	27
Sep	5	906	−11	2	3

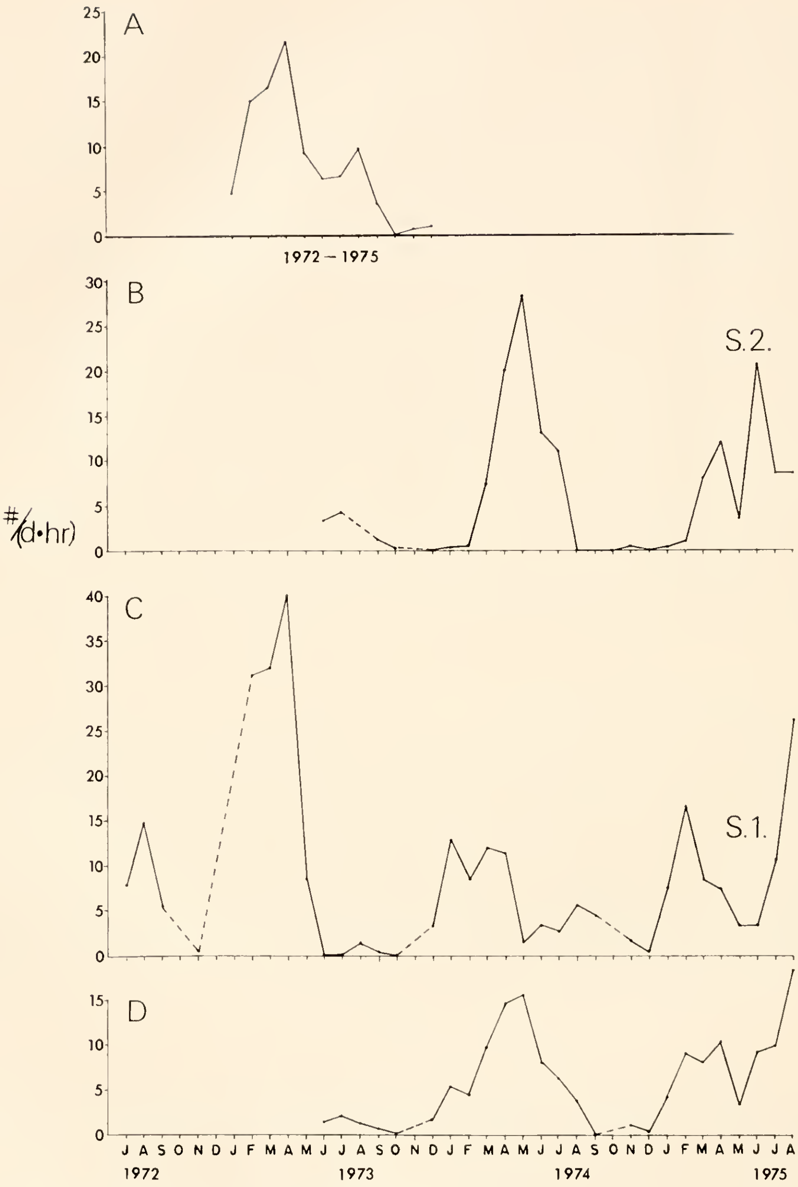

FIGURE 4. Abuandance of animals expressed as *Aplysia* per diver-hour, plotted against the month. A: data from both study sites over the entire collection period are combined in a single "composite year". B: abundance at Site 2 plotted against actual time. C: abundance at Site 1 plotted against actual time. D: average abundances for both sites graphed for that period during which both sites were sampled. Dotted lines indicate that one or more collections were missed during the period covered.

and *Laurencia* brought into the laboratory. Juveniles very similar in color to the red algae were found hidden among the fronds, and these small animals seemed to be especially abundant during fall, winter and early spring.

Although distinct trends emerged from the total data collected (Figure 4A), Figures 4B, C and D show the considerable variability of the two sites from year to year. For example, collections at Site 1 during June, July and August 1973 produced a total of five individuals, while collections during the same months of 1975 produced 183 animals (including 25 recaptures).

A predictable occurrence at both sites was the nearly total disappearance of animals in the fall (October through December). Many individuals collected during this period exhibited symptoms of physical deterioration. These included erosion of the free edges of the parapodia and loss of pigment resulting in pale patches on the body. Such animals frequently died in captivity, an unusual occurrence at other times of the year. Few dead animals were found in the field at any time of the year.

Reproductive activity

When collections were initiated at Site 1 in July of 1972, copulation was already in progress. The following year, no copulation or egg-laying was observed there due to the disappearance of the population in June (May was the last successful collection in 1973 at Site 1, and no mating was observed at that time.) Collections at Site 2 began in June 1973, at which time copulation was occurring. In 1974, a few large animals were first seen mating in April at Site 1, and in May at Site 2. In 1975, again a few large animals were seen mating at Site 2 as early as April, but at Site 1, copulation and egglaying were not observed until July, at which time many animals were participating.

Data on the percentage of animals aggregated, and the number of animals making up aggregations, are plotted in Figure 5. In April and May, the percentage of animals observed in pairs and aggregations was small, but increased to 80% or more during the months of July and August (Fig. 5A). Fifty-three aggregations are plotted according to the number of animals participating (Fig. 5B), which ranged from 2 to 19. Pairs of animals were observed more frequently than any other size grouping. Since *Aplysia* mates in chains of indefinite length, a pair of animals may be considered the shortest possible mating chain.

Seasonal changes in oocyte diameter

The data graphed in Figure 6 show the changes in oocyte diameter which underlie seasonal breeding in *A. californica*. Most animals collected in winter (January through March) have extremely small gonads containing few recognizable oocytes, these averaging about 7 μm in diameter. In April and May, the gonad is characterized by a mixture of oocytes of all sizes, ranging up to 80 μm, the approximate diameter of a newly laid ovum. The proportion of large oocytes increases with time, until, by the months of September, October, and November, mature animals show few of the small oocytes which predominate in the spring. The low standard error in average oocyte diameter in animals collected between January and October inidicates that oocyte maturation is relatively synchronized. In November and

December, the standard error increases due to the inclusion of some sexually immature animals. It should be noted that, during the winter months, size is not an accurate indicator of sexual maturity. Sexually immature specimens of up to 600 g have been found at this time.

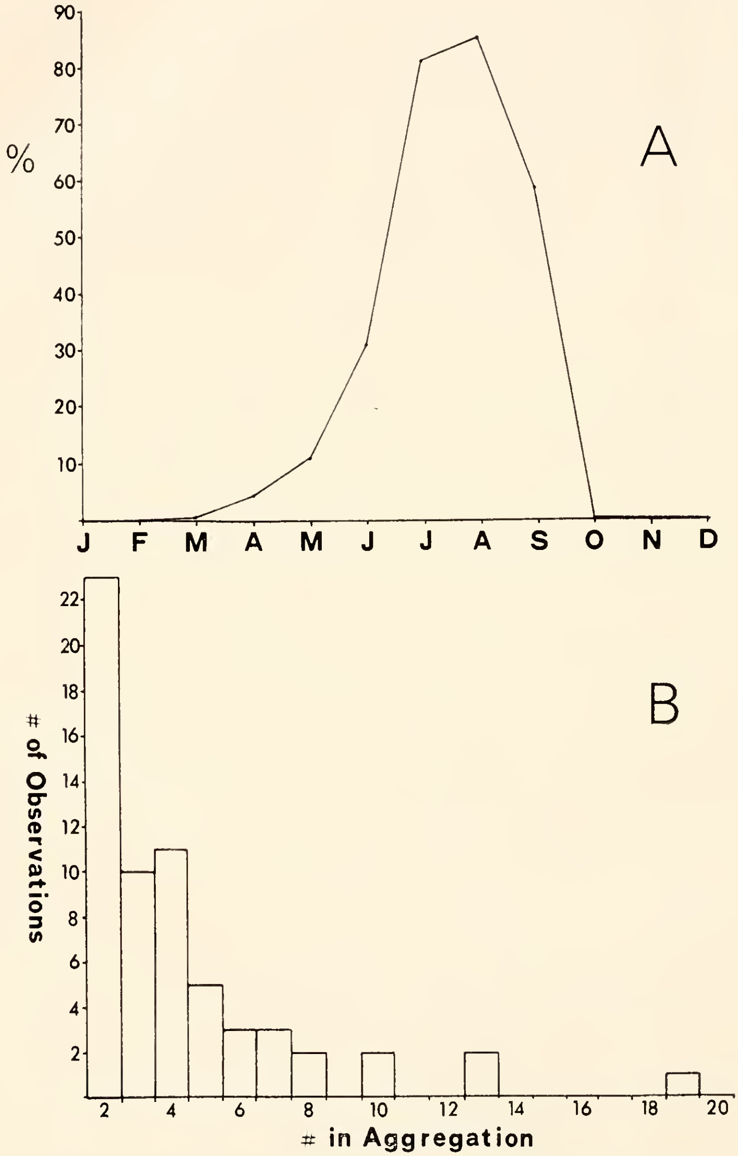

FIGURE 5. A: percentage of the total number of specimens of *Aplysia* captured each month that were paired or aggregated. Data from both study sites throughout the collection period are combined. B: frequency of observation of aggregation plotted against aggregation size.

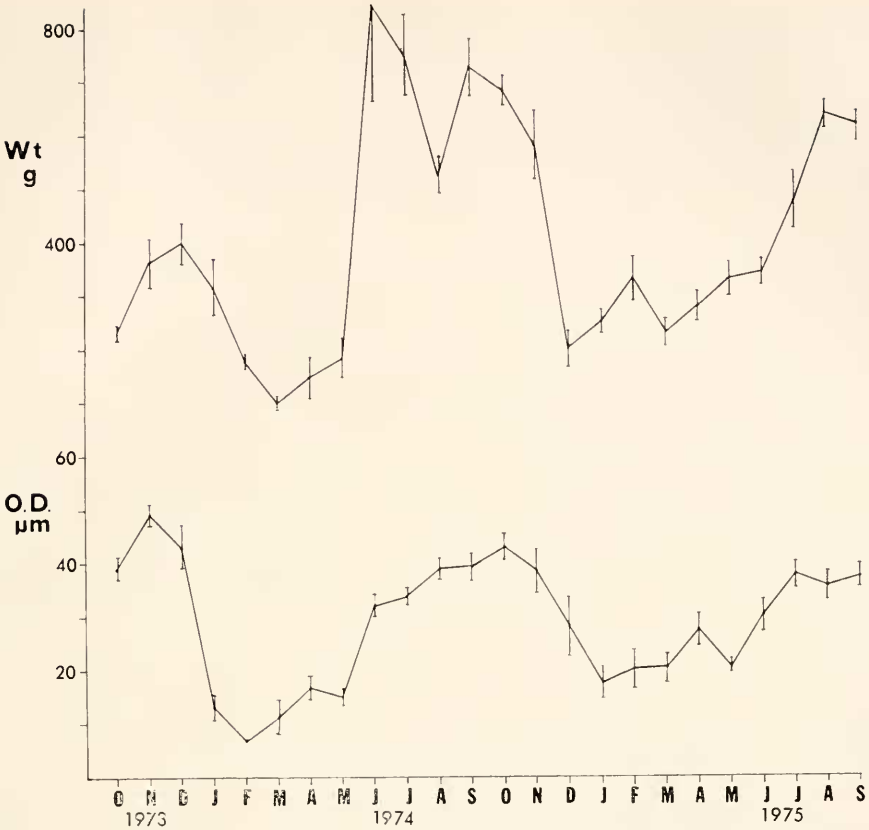

FIGURE 6. Mean weights (upper line) and oocyte diameters (lower line) of specimens of *Aplysia* plotted against time. These animals were collected at Palos Verdes, California, by Pacific Biomarine Supply Co. Most data points represent at least 10 individuals (see text). These were sacrificed throughout the month indicated, and collected an average of 11 days prior to being killed. Bars indicated standard error of the mean.

DISCUSSION

Data presented in this paper support the hypothesis that *Aplysia* have a life expectancy of approximately one year, and a single extended period of copulation and egglaying which begins late in spring and ends in the fall with the death of the sexually mature population. Although migration into deeper water and reappearance in the spring cannot be entirely ruled out, there is presently no evidence in support of this hypothesis. Animals found in the spring tend to be smaller and more abundant than those found later in the year. They appear healthy and live for long periods under laboratory conditions, in contrast to animals obtained in the fall whose skin is often eroded and who usually die after a short period of captivity.

The extended period of egg production might be expected to result in asynchrony with respect to size and sexual maturity within the population. However, there is evidence that increasing water temperature in the spring provides a synchronizing cue for the initiation of gonadal development (Audesirk, 1976; Smith and Carefoot, 1967). Differences in survival and growth rate during different seasons might also result in greater uniformity in size than would be predicted from the long period of egglaying. Further study is required to test these hypotheses. The disappearance of nearly all animals larger than 20 g at Catalina Island as early as October is in contrast to the situation at Palos Verdes where sexually mature specimens are found until December. A comparison of environmental factors including water temperature, food availability, and wave exposure between the two locations might provide clues to this discrepancy.

The mean weights of the populations at Palos Verdes and Catalina show pronounced seasonal differences consistent with an annual species (Figures 1, 2, and 6). On Catalina, small specimens of *Aplysia,* presumably offspring of the previous reproductive season, make their appearance between January and May. Maximum size is reached in June or July, and shows a decrease in August and September. In October, November and December, few animals are found (Fig. 4). Although trends in mean weight were roughly parallel for the two Catalina Island populations sampled, a consistent and significant size difference was observed (Fig. 2). The apparent explanation for this is the relative availability of food algae at the two sites. At Site 1, no algal species known to be readily consumed by *Aplysia* under laboratory conditions was found in abundance. In contrast, Site 2 included large beds of the red alga *Plocamium* which *A. californica* will eagerly consume. In his study of *A. punctata,* Carefoot (1967a) found a strong correlation between the size of the animals and the abundance of *Plocamium.* In a comparison of eight algal species consumed by *A. punctata, Plocamium* was preferred over six other species, and supported most rapid growth (Carefoot, 1967b).

Data from tagging and recapture (Fig. 3; Table I) indicate that, at Catalina Island, *A. californica* experiences fastest growth between February and April, prior to the onset of breeding. The animal's capacity for rapid growth explains how some individuals may achieve sizes in excess of 3000 g in a single year. Growth slows as breeding intensity increases, and the average size reaches a peak in June or July. In August, when breeding is at its most intense (as indicated by the percentage of animals in pairs or aggregations in Fig. 5), a net loss of weight occurs. This loss is possibly attributable to two major causes. The first is loss of foraging time due to time spent in reproductive activities. Although the percentage of time spent in breeding has never been quantified, field observations indicate that individuals could remain in aggregations for a day or longer. Kupfermann and Carew (1974) tagged the five animals at one aggregation site and, during four visits during the next five days, always observed one or more tagged animals at the site. The animals were not individually identified, and some had certainly departed and returned, but others may have remained. Aggregations and pairs of individuals appear almost exclusively during months when copulation is observed. It is hypothesized that the animals in aggregations which are not engaged in egglaying or copulation at any given time may have recently completed one or more of these activities, or may be about to engage in them. Further study is needed to test this hypothesis. During the present study, at Site 1 nearly all the mating aggregations were discovered in dense beds of the surfgrass *Phyllo-*

spadix, whose closely spaced blades seem to present an ideal anchoring site for the tangled egg masses. Since they do not consume this plant, the animals at Site 1 probably did not eat during the time spent in aggregations. Kupfermann and Carew (1974) also never observed feeding by animals in breeding aggregations.

The second major factor contributing to weight loss is the massive egg production by these hermaphrodites (MacGinitie, 1934) which requires large energy expenditures.

Although seasonal trends in abundance are evident, these are superimposed upon dramatic fluctuations from one year to the next. Beeman (1977) noted that opisthobranch populations "tend to be erratic and sporadically explosive," a generalization with some applicability to *Aplysia.* Eales (1921) and Carefoot (1967a) reported similar fluctuations in populations of *A. punctata.*

Like *A. punctata,* which is found dead or dying in the field between September and December (Carefoot, 1967a), *A. californica* shows physical deterioration manifested externally as tissue erosion during the same months. A related phenomenon was reported by Lickey, Wozniac, Block, Hudson, and Augter (1977), who noted that specimens of *A. californica* in the laboratory seldom die between December and July, but rarely survive more than a month between August and November. For unknown reasons, dead animals were rarely found in the field at Catalina Island. In the laboratory, however, death was common during these months.

The brief life cycle of *A. californica* and the dramatic changes in its physiology and behavior as it progresses from sexual immaturity through the reproductive state to senescence have important implications for investigations of *Aplysia* neurobiology. Changes in neurohormones with respect to season have already been noted (Strumwasser, Jacklet, and Alvarez, 1969). The formation of breeding aggregations, copulation, and egglaying are dramatic behavioral changes correlated with sexual maturity. The imminent death of mature animals obtained in the fall must also be taken into account during investigations of *Aplysia* behavior and nervous system function.

Summary

1. Observations of field growth rates, reproductive activities, and abundance of *Aplysia calfiornica* were made over a three-year period on Santa Catalina Island off southern California.

2. The mean weight of the population was found to vary with the location in which the animals were collected, presumably as a result of differing availability of food.

3. Seasonal weight differences were also apparent. In general, small specimens of *A. californica* appear between February and May. Mean weight reached a maximum between June and August. Considerable variability was encountered from year to year.

4. Tagging and recapture showed that growth rates reached a maximum in the spring just prior to breeding. The rate decreased thereafter until weight loss was experienced in August and September.

5. *A. californica* was usually most abundant in the spring, with numbers decreasing during the summer. The animals almost completely disappeared during the months of October, November, and December with the exception of extremely small specimens found on algae.

6. Breeding activity was occasionally observed as early as April and reached its greatest intensity during July and August when at least 80% of the animals collected were in breeding aggregations.

7. Histological examination of gonads showed maximum oocyte diameter between June and October, and minimum between January and March.

8. Data are consistent with an annual species whose extended summer breeding period is terminated by the death of mature individuals during the fall.

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